THE FIRST MESOZOIC SOLIFUGAE (ARACHNIDA), FROM THE CRETACEOUS OF BRAZIL, AND A REDESCRIPTION OF THE PALAEOZOIC SOLIFUGE

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ABSTRACT. The first Mesozoic solifuge, from the Early Cretaceous (Aptian) Crato Formation of Ceará province, Brazil, is described and named as *Cratosolpuga wunderlichi* Selden, gen. et sp. nov. and placed in the extant family Ceromidae. There are two previously described fossil solifuges: from Palaeogene Dominican amber and the Carboniferous (Westphalian D) Francis Creek Shale of Mazon Creek, Illinois. The latter specimen (*Protosolpuga carbonaria*), redescribed herein, is poorly preserved but provides evidence for the presence of the order in the Carboniferous.

THE fearsome appearance of solifuges, with their enormous chelicerae and swift movements, ensures their familiarity among the inhabitants of desert regions of the world. None of their numerous vernacular names, for example camel-spiders, sun-spiders, Roman-spiders and wind-scorpions, is really appropriate. Most solifuges are nocturnal, but some emerge from their burrows to hunt in the daytime. Solifuges generally use their chelicerae for digging (Pocock 1897; Hewitt 1919, p. 19), although the short legs with rows of stiff spines of Hexisopodidae are adapted for rapid locomotion through sand (Cloudsley-Thompson 1977). The great speed of solifuges when disturbed is legendary, and with their profuse, long hairs, many species appear like tufts of thistledown blowing in the wind as they run across the ground. Solifuges are generalist predators: their prey includes spiders, grasshoppers, termites (Pocock 1897), and other insects (Punzo 1994), and even scorpions, mice, lizards, and birds (Cloudsley-Thompson 1977). Apparently, prey is detected and captured with the pedipalps, then killed and masticated with alternate, scissor-like movements of the powerful chelicerae, which lack venom.

Protosolpuga carbonaria Petrunkevitch, 1913, from the Upper Carboniferous (Westphalian D) of Mazon Creek, Illinois was the only fossil solifuge known until Poinar and Santiago-Blay (1989) described a specimen from Tertiary Dominican amber as *Happlodontus proterus*. *Protosolpuga* was described by Petrunkevitch (1913, p. 74) as being in a very poor state of preservation. Our study confirms this, and gives a new interpretation of the fossil, which is nevertheless just recognizable as a solifuge.

A new solifuge is described here (Text-fig. 1), from two specimens preserved in exceptional detail in the Crato Formation, Cretaceous of Brazil. They are the first known from Mesozoic strata. The only previous records of Brazilian solifuges are Recent Ammotrechidae and Mummuciidae from the south-east of the country (Maury 1984). Indeed, north-eastern Brazil is farther geographically from any previous solifuge record within the tropics.

Terminology

The ordinal name Solifugae is used in preference to Solpugida on the recommendation of the Centre International de Documentation Arachnologique. For solifuge terminology, we have mainly followed Muma (1951). A recent reinterpretation of solifuge appendages by Shultz (1989, 1990) concluded that the classical terminology applied to solifuge podomeres was based on erroneous
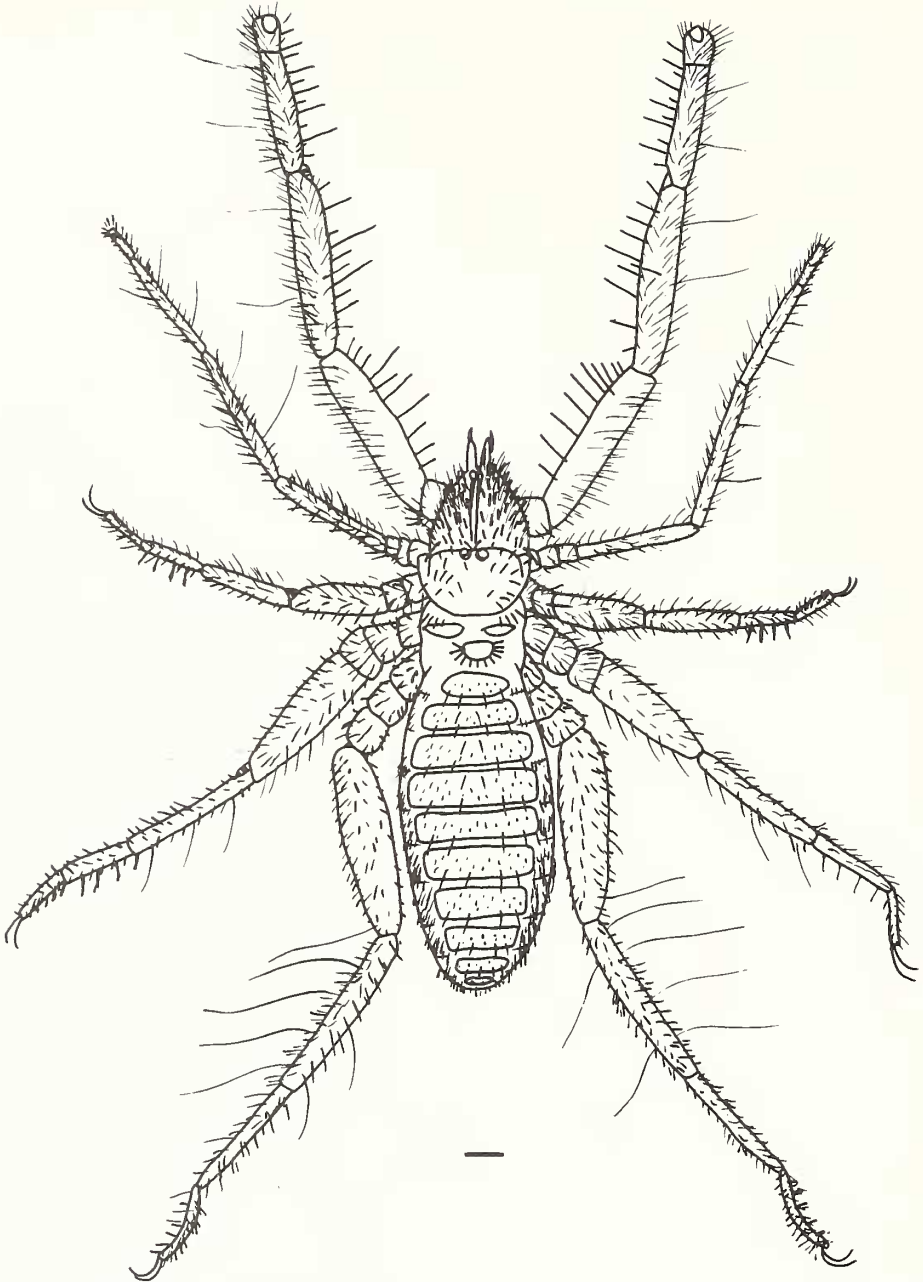
TEXT-FIG. 1. Reconstruction of *Cratosolpuga wunderlichi* Selden, gen. et sp. nov., Cretaceous (Aptian), Crato Formation, Ceará Province, Brazil, illustrating general appearance of solifuges. Scale bar represents 1 mm.

homology. We follow Shultz's terminology here, and a comparison of the terms is given in Table 1. Description of the Carboniferous solifuge was prepared by WAS; that of the Cretaceous solifuge by PAS, who is also responsible for the Systematic Palaeontology. Abbreviations used in the Text-figures are as follows:

1–10	opisthosomal sternite numbers	mp	mesopeltidium
1, II, III, IV	leg numbers	mtp	metapeltidium
ar p	arcus posterior (of parapeltidium)	op	opisthosoma
ch	chelicera	operc	operculum
cx	coxa	pa	patella
el	exterior lobe (of propeltidium)	pd	pedipalp
f fi ch	fixed finger of chelicera	pp	propeltidium
fe	femur (legs I, II)	st	sternal plate between coxae I (tritosternum)
fe1, fe 2	basifemur, telofemur (legs III, IV)	ta	tarsus of pedipalp
fl	flagellum	ta1, ta2	basitarsus, telotarsus of legs
m fi ch	movable finger of chelicera	ti	tibia
ma	malleolus (racquet organ)	ti trich	tibial trichobothrium
med pl	median plagula (of parapeltidium)	tr	trochanter

TABLE 1. Comparison of Shultz's (1989) solifuge podomere terminology with that of Roewer (1934)

| Pedipalp		Legs I and II		Legs III and IV	
Shultz	Roewer	Shultz	Roewer	Shultz	Roewer
Coxa	Coxa	Coxa	Coxa	Coxa	Coxa
Trochanter	Trochanter	Trochanter	Trochanter	Trochanter	Trochanter 1
Femur	Femur	Femur	Femur I	Basifemur	Trochanter II
Patella	Tibia	Patella	Femur II	Telofemur	Femur I
Tibia	Metatarsus	Tibia	Tibia	Patella	Femur II
Tarsus	Tarsus	Basitarsus	Metatarsus	Tibia	Tibia
Apotele	Pretarsus	Telotarsus	Tarsus	Basitarsus	Metatarsus
—	—	Apotele	Pretarsus	Telotarsus	Tarsus
—	—	—	—	Apotele	Pretarsus

PROTOSOLPUGA CARBONARIA

Material

The holotype and only known specimen of this arachnid (Peabody Museum, Yale University, 00155/B1336; Pl. 1, figs 1–2; Text-fig. 2) comes from the Carboniferous (Westphalian D) of Mazon Creek, Illinois. It is preserved in a siderite (iron carbonate) nodule characteristic of that locality, with both halves preserved. Despite the poor preservation, each half of the nodule preserves a mixture of dorsal and ventral features. Petrunkevitch's drawing (1913, fig. 40) is highly diagrammatic and shows a few features that cannot now be seen on the specimen. Conversely, some features that appear obvious on the specimen now are not on his drawing. On one half, the most obvious feature is a large structure with deformed small ridges at the distal end, which Petrunkevitch interpreted as the chelicerae; because most of the structures that can be made out on this half appear to be ventral ones, this side is here designated the ventral half, and the other the dorsal half. Petrunkevitch's drawing is a composite of both surfaces, with some features shown on the dorsal half reversed.

Morphological interpretation

The ventral half preserves the body and at least six appendages of an arachnid. Anteriorly, the fossil displays a small arrangement of twisted ridges forming a distal structure on a pear-shaped mass that appears to have a central dividing groove. This was interpreted by Petrunkevitch (1913) as the large chelate chelicerae of a solifuge; the ridges to which he referred were thought to represent the
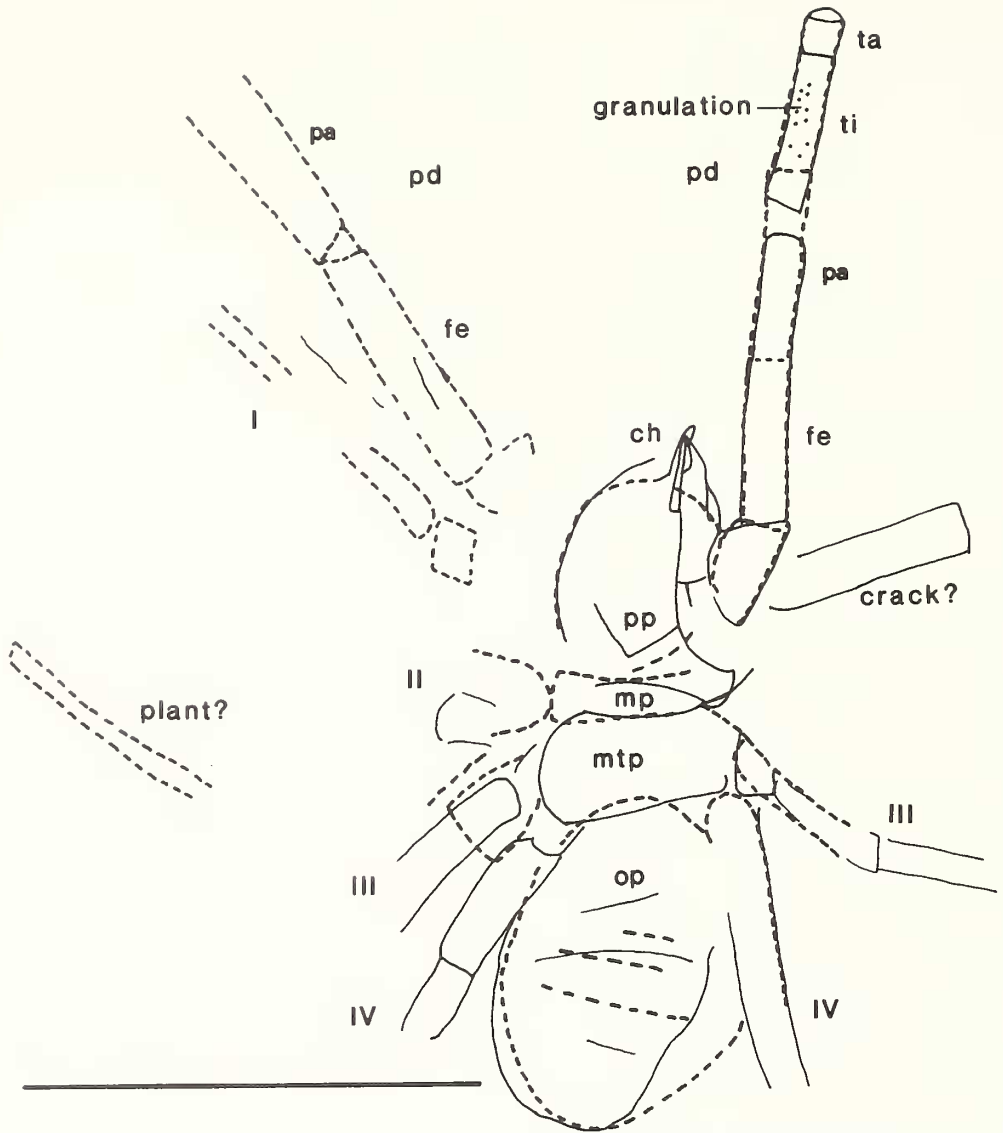
TEXT-FIG. 2. Composite camera lucida drawing of *Protosolpuga carbonaria* Petrunkevitch, 1913. Holotype, Peabody Museum 00155/B1336; Upper Carboniferous (Westphalian D), Francis Creek Shale; Mazon Creek, Illinois. Solid lines, ventral side; dashed lines, dorsal side. Scale bar represents 10 mm.

cheliceral fingers. Petrunkevitch referred to and illustrated 'a row of punctuations' on each finger, but these cannot now be detected. Behind the supposed chelicerae, the outlines of a broad plate can be discerned, separated from the cheliceral bases by a short space. This may be a dorsal structure, the tergite of the metapeltidium. The abdomen is an oval roughly twice as long as wide, with only a few vague lines possibly indicating segmentation. In this area there is some carbonized material and several clusters of pyrite crystals. Lateral to the chelicerae on one side is a large pedipalp coxa, from which extend distal segments of the leg-like pedipalp. Little detail is visible and the segmentation of the pedipalp cannot be made out clearly on either half of the nodule. However, at

the end of the preserved portion, as Petrunkevitch noted, there is a short podomere about as wide as long, with a distal concavity. This is consistent with the small pedipalp tarsus of a solifuge, which bears a distal, eversible membranous sac. If this interpretation is correct, the next proximal segment is the tibia. On the ventral half, a series of small granulations (Text-fig. 2) can be seen, and these are reflected on the dorsal half by a series of small pits in the corresponding positions. Stout spines are borne on the tibiae of some living solifuges, and these pits may represent their sockets. The other appendages that are preserved are presumed to be legs; the presence of four pairs can be confirmed by combining information from both halves.

On the dorsal half, the chelicerae do not appear as clearly as on the ventral half; one sees only a rounded mass with a vague outline. However, under alcohol, contrast between small areas of carbonized material and the reddish matrix is enhanced, and there appears to be a transverse divide which could separate the cheliceral bases from the propeltidium. Approximately in the anterior midline is a small carbonized knob; this is in the position of the median eye tubercle in living solifuges. Petrunkevitch (1913) stated flatly 'eyes absent' but presumably he meant that he could detect no evidence for eyes. Behind the possible propeltidium is a narrow band which could be the tergite of the mesopeltidium. The metapeltidium does not appear on this half of the nodule. The abdomen looks about the same as on the ventral half. The dorsal half preserves more of the legs and parts of both pedipalps. At least the first leg is more slender than the pedipalps, but the third leg also appears as gracile as the first. What appear to be the remnants of fourth legs are about half as robust. On both halves there is an elongate structure some distance from the specimen which was obviously considered by Petrunkevitch to be a distal leg segment. However, it has quite a different texture from the rest of the fossil and is probably a plant fragment.

The cheliceral punctuations depicted by Petrunkevitch cannot be seen. Mysteriously, he mentioned 'three free thoracic segments', but in living solifuges there are only two, the meso- and metapeltidia. Petrunkevitch's drawing actually shows four, not three, of these segments, but there is no evidence for any more than the expected two, taking into account that both halves of the nodule preserve both dorsal and ventral structures. The 'even segmentation' of the pedipalps is not really clear; at least one of the 'joints' is due to a crack in the matrix. On the right side of Text-figure 2 the large cylindrical structure extending from the pedipalp coxa at about 70° to the pedipalp, and considered by Petrunkevitch as part of a leg, is very probably due to cracking of the nodule. Three short, narrow pieces, considered by Petrunkevitch as legs, are found in his illustration. One of these is the aforementioned bit of plant debris; the other two cannot be found under any conditions of lighting. These were probably the evidence for Petrunkevitch's characterization of the second legs as 'considerably thinner than the others'. In fact, it would appear that only the coxa of the second leg on the right side is preserved, so nothing can be said about their relative robustness. Petrunkevitch also depicted the first leg (on the left side of Text-fig. 2) as nearly as robust as the pedipalp; in reality it is only about half as thick. The segmental lines shown by Petrunkevitch and his description of the abdomen as consisting of seven segments is not supported by evidence. There are few possible segmental lines visible and even these could be attributable to folding of the soft abdomen or other factors. In any case, modern solifuges have a typical 11-segmented abdomen, and it would be remarkable if this were not the case in the Carboniferous forms as well.

Discussion

Of the orders of Arachnida supposedly known from the Carboniferous, only spiders, trigonotarbids and solifuges (represented only by the present specimen) have leg-like pedipalps. Spider and trigonotarbid pedipalps are shorter than the legs. *Protosolpuga carbonaria* clearly shows a leg-like pedipalp that is equal to or even larger than the walking legs. In addition, a small, button-like tarsus appears to be present. If the interpretation of the anterior structure as the chelicerae is correct, and if there are two free thoracic segments, this is additional evidence that the specimen really does represent a solifuge.

The level of preservation is so poor that the fossil tells us little about solifuge evolution. Perhaps it should be expected that, like other orders of arachnids, Solifugae had assumed a fully modern form by Carboniferous times.

THE CRETACEOUS SOLIFUGE

Geological setting

The solifuge specimens originate from the Crato Formation (*sensu* Martill 1993), a sequence of laminated, organic-rich micrites (Plattenkalk), which crop out on the north side of the Chapada do Araripe in north-eastern Brazil, dated tentatively as Aptian (Maisey 1990; Martill 1993). The Crato Formation is rich in insects (Grimaldi 1990), and also contains the small fish *Dastilbe*, land plants (including angiosperms), other arachnids (including spiders, scorpions, uropygids and opilionids), frogs, and bird feathers, but no terrestrial or flying reptiles (Martill 1993). The palaeoenvironment is presumed to be lacustrine, the majority of the biota is allochthonous, being blown or washed into the lake or, if aquatic, subject to mass morality (Maisey 1990; Martill 1993).

The Crato Lake formed within the Aquatic Basin, one of a number of fault-bounded Mesozoic basins in what is now north-eastern Brazil which occupied the Atlantic rifting zone between Africa and South America in early Cretaceous times. The fault lines in this part of Brazil align with the Benue Trough and other lineaments in West Africa, and it is suspected that these older faults were reactivated to become transforms at the onset of rifting (Berthou 1990). As far as the solifuge is concerned, its contemporaries could have moved freely overland between what are now the African and American continents.

Taphonomy

No chemical analyses were carried out on the specimens, but, in comparison with the insects preserved in the Crato Formation (Grimaldi and Maisey 1990), we presume that the solifuge fossils are preserved in goethite (hydrated iron oxide) in a matrix of nearly pure calcite mud with clots of pyrolusite. The goethite is a tan colour which is darker where thicker and thus reflects the depth of coloration seen in the original cuticle. The mineralization appears to have replaced the original organic material in great detail, so that spines, bristles, and fine trichobothria can be traced accurately in the matrix. Where absent, the former presence of spines and trichobothria is indicated by spine bases and bothria on the cuticle surface. The membrane on the cheliceral flagellum of the holotype is preserved almost intact. Where the podomere cuticle is broken through on the femur of the right pedipalp of the holotype, a structure interpreted as a tendon can be seen. It is clear that the preserved parts represent material of originally cuticular composition (e.g. tendons) because most of the fossil is crushed to some extent, and no evidence of internal soft tissues (e.g. muscles) can be seen.

EXPLANATION OF PLATE 1

Figs 1–2. *Protosolpuga carbonaria* Petrunkevitch, 1913. Holotype; Upper Carboniferous (Westphalian D), Francis Creek Shale; Mazon Creek, Illinois; Peabody Museum 00155/B1336. 1, part (mainly ventral). 2, counterpart (mainly dorsal); × 4·5. See Text-figure 2 for explanation.

Fig. 3. *Cratosolpuga wunderlichi* Selden, gen. et sp. nov. Additional (juvenile) specimen; Cretaceous (Aptian), Crato Formation; Ceará Province, Brazil; SMNK 1268 PAL in Staatliches Museum für Naturkunde, Karlsruhe; dorsal view of ventral structures; × 9·5. See Text-figure 3 for explanation.

Fig. 4. *Cratosolpuga wunderlichi* Selden, gen. et sp. nov. Holotype; Cretaceous (Aptian), Crato Formation; Ceará Province, Brazil; Sol 1 in the Wunderlich Collection; dorsal view of prosoma omitting distal parts of appendages; × 11·4. See Text-figure 4 for explanation.

PLATE 1

SELDEN and SHEAR, Solifugae

Material and methods

The holotype (Pl. 1, fig. 4; Pl. 2; Text-figs 4–6) consists of a single slab of laminated, pinkish buff limestone with the fossil on the presumed upper surface. The lower half of the slab is brownish buff limestone, and the lower surface is thickly strewn with clots of dendritic pyrolusite. No other fossils are present on the slab. The pinkish upper half of the slab has been broken, and repaired with glue. The break is visible as a sinuous crack across the middle of the specimen, cutting the proximal podomeres of legs III and IV and the basitarsus and telotarsus of right leg II. Some careful preparation was necessary to expose fully details of the specimen, such as the lateral parts of the chelicerae and propeltidium and tarsal claws. This was accomplished using a combination of dilute hydrochloric acid (used sparingly and of only little aid to preparation) and mechanical scraping. A very fine, steel hypodermic needle was connected to the polythene tubing of an air pump of the type intended to aerate small indoor aquaria. The matrix was loosened gently using the bevelled tip of the hypodermic needle under the binocular microscope (× 40– × 60). The advantage of this over a simple fine needle is that loosened particles of matrix are blown away immediately, revealing the specimen beneath. Also, the loose grains themselves gently dislodge other particles around the area, so that the working site is always clean.

   The second specimen (Pl. 1, fig. 3; Text-fig. 3) is about one-quarter the size of the holotype, and is presumed to be a juvenile. It is preserved as an external mould with fragments of cuticle, spines and setae adhering. It preserves the ventral side of the prosoma and abdomen and all appendages. It therefore complements the holotype in providing details of parts of the body which are missing from the latter. Little preparation was carried out on the second specimen.

   Modern solifuges were studied for comparative purposes. Undetermined specimens of families Solpugidae and Galeodidae were available, together with adult males of Solpugidae, *Ceroma ornatum* Karsch, 1885 (Ceromidae) and *Blossia sabulosa* (Lawrence, 1927) (Daesiidae). A female ceromid, lacking data but identified using Roewer (1934) as *C. ornatum*, was also studied.

Morphological interpretation

The fossils appear remarkably modern in aspect; the morphology is essentially similar to that of a modern solifuge, and they have been interpreted in this light (Text-fig. 1). A few critical features are discussed below, with reference to the holotype unless stated otherwise.

Propeltidium and associated tergites. The propeltidium of *Cratosolpuga* gen. nov. is wider than long. The anterior margin is very slightly recurved. The anterior edge is clearly rebordered, a feature which continues posterolaterally adjacent to the exterior lobe. The exterior lobe is strongly raised into a pyramidal shape. The exterior lobe is clearly separated from the main part of the propeltidium except posteriorly; presumably in life it was free except posteriorly, an arrangement found in numerous families of modern solifuges. The posterior margin is procurved into a semicircle. The boundaries of the tergites posterior to the propeltidium are not entirely clear. The most obvious structure is a pair of high, steep-sided transverse ridges. These ridges almost certainly correspond to the anterior edges of the left and right arcus posterior of the propeltidium. Anterior to the ridges is a crescentic area which corresponds to the median plagula and arcus anterior of the propeltidium. Behind the propeltidium the ridges fall steeply to the basal podomeres of leg III and, medially, a semicircular structure with radiating spines which corresponds to the mesopeltidium (= penultimate prosomal tergite).

EXPLANATION OF PLATE 2

Fig. 1. *Cratosolpuga wunderlichi* Selden, gen. et sp. nov. Holotype; Cretaceous (Aptian), Crato Formation; Ceará Province, Brazil; Sol 1 in the Wunderlich Collection; complete specimen seen from dorsal aspect; × 4·7. See Text-figure 5 for explanation.
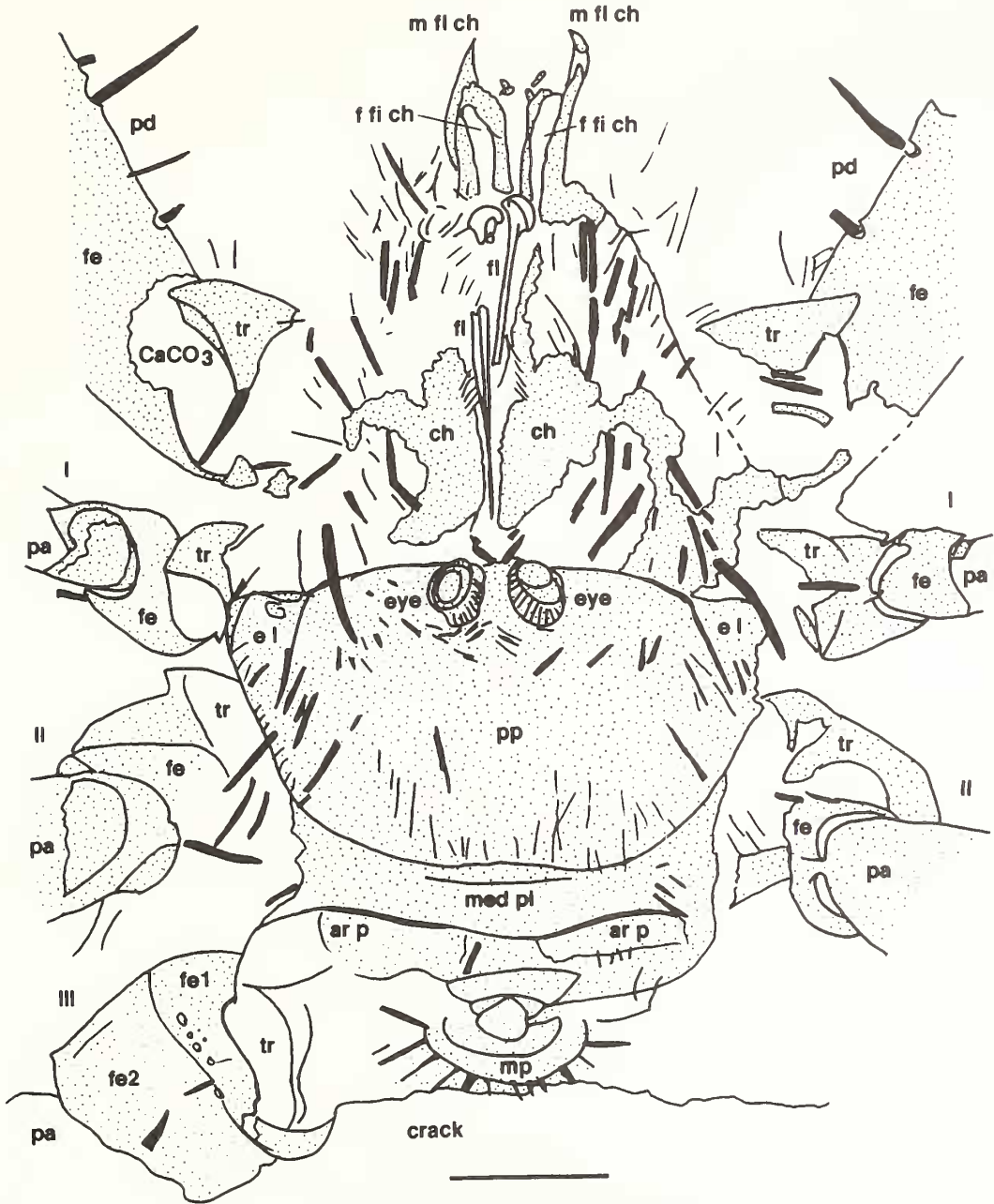
PLATE 2


SELDEN and SHEAR, *Cratosolpuga*
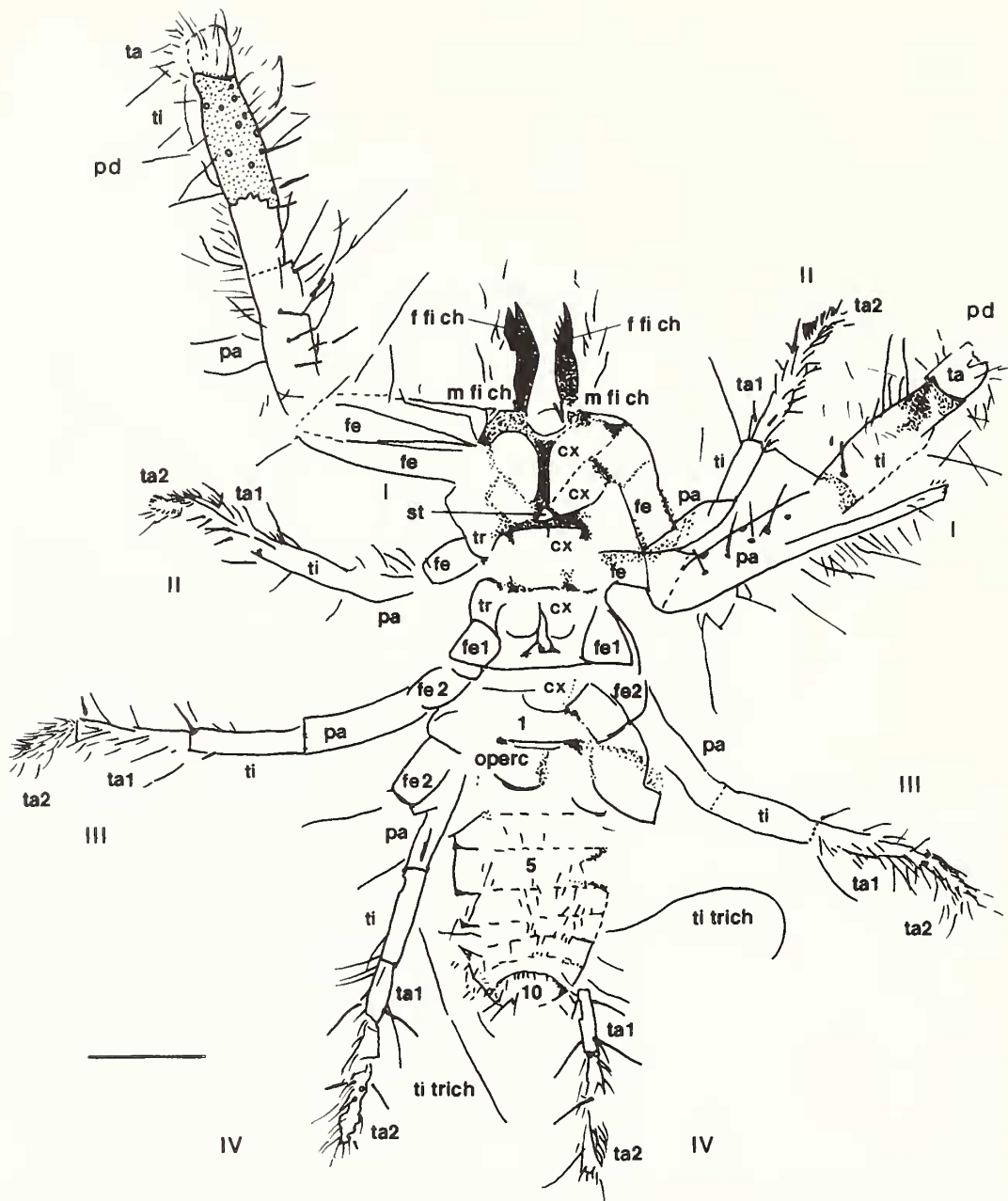
TEXT-FIG. 3. Camera lucida drawing of *Cratosolpuga wunderlichi* Selden, gen. et sp. nov. Additional (juvenile) specimen; Cretaceous (Aptian), Crato Formation, Ceará Province, Brazil; SMNK 1268 PAL in Staatliches Museum für Naturkunde, Karlsruhe. See Plate 1, figure 3. Scale bar represents 1 mm.

Chelicerae. The chelicerae were clearly bulbous in the proximal part, but narrow considerably at the base of the dorsal fixed finger. The dorsal side of the fixed finger has a concavity which contains calcite grains; the distal (anterior) end of the fixed finger appears to be broken off. This observation leads to a number of possible conclusions.

TEXT-FIG. 4. Camera lucida drawing of prosoma (omitting distal parts of appendages) of *Cratosolpuga wunderlichi* Selden, gen. et sp. nov. Holotype; Cretaceous (Aptian), Crato Formation; Ceará Province, Brazil; Sol 1. Dotted regions are exposed cuticle (preserved in goethite); strong spines shown in black; flagella ornamentation not shown, for clarity. Scale bar represents 1 mm.

First, there may have been a real concavity in life; this would explain the grains of matrix within the concavity. Some eremobatids (Muma 1951) bear dorsal concavities on the fixed finger; such concavities are normally not on the dorsal side of the finger, however. Secondly, it could represent

10 mm
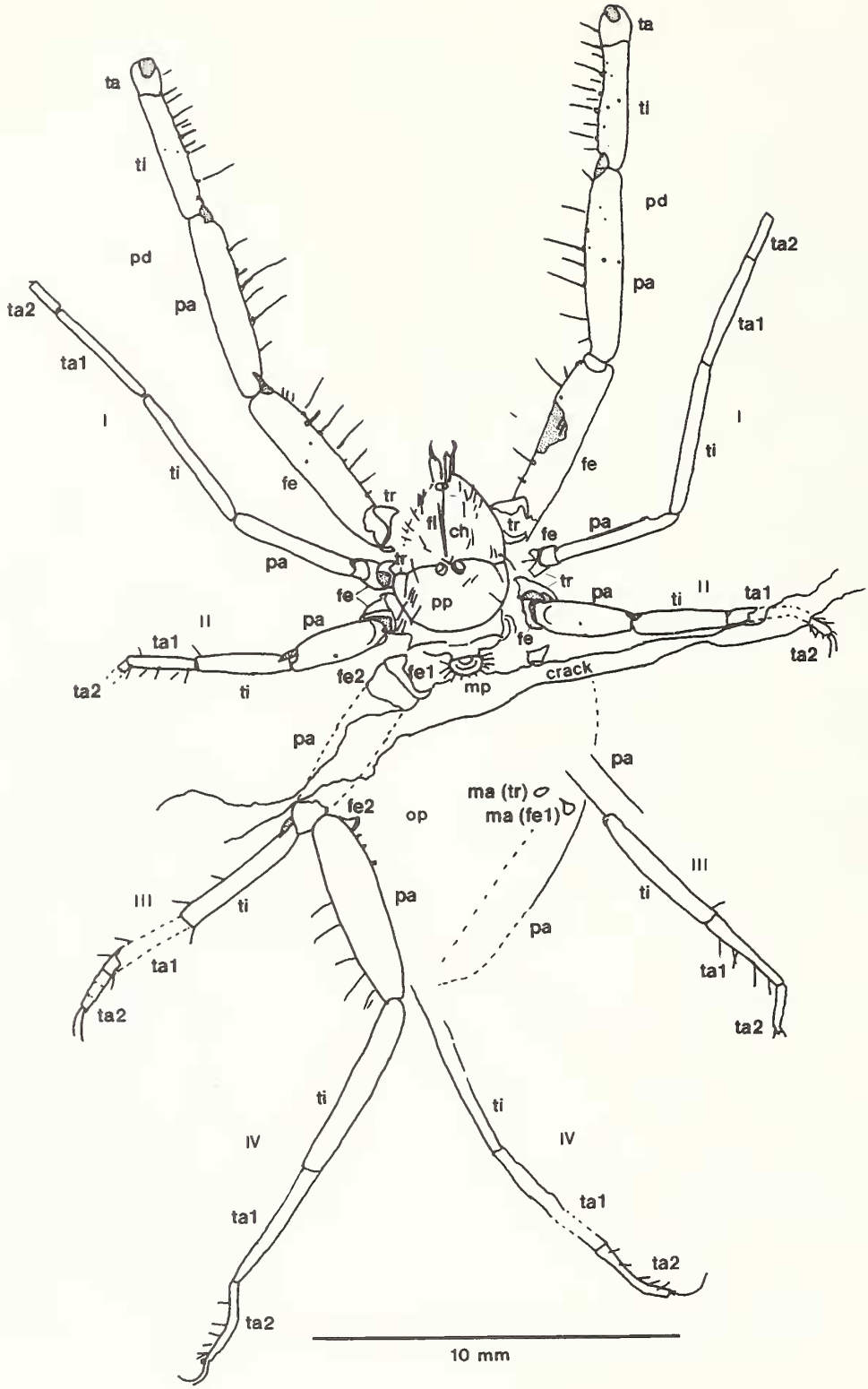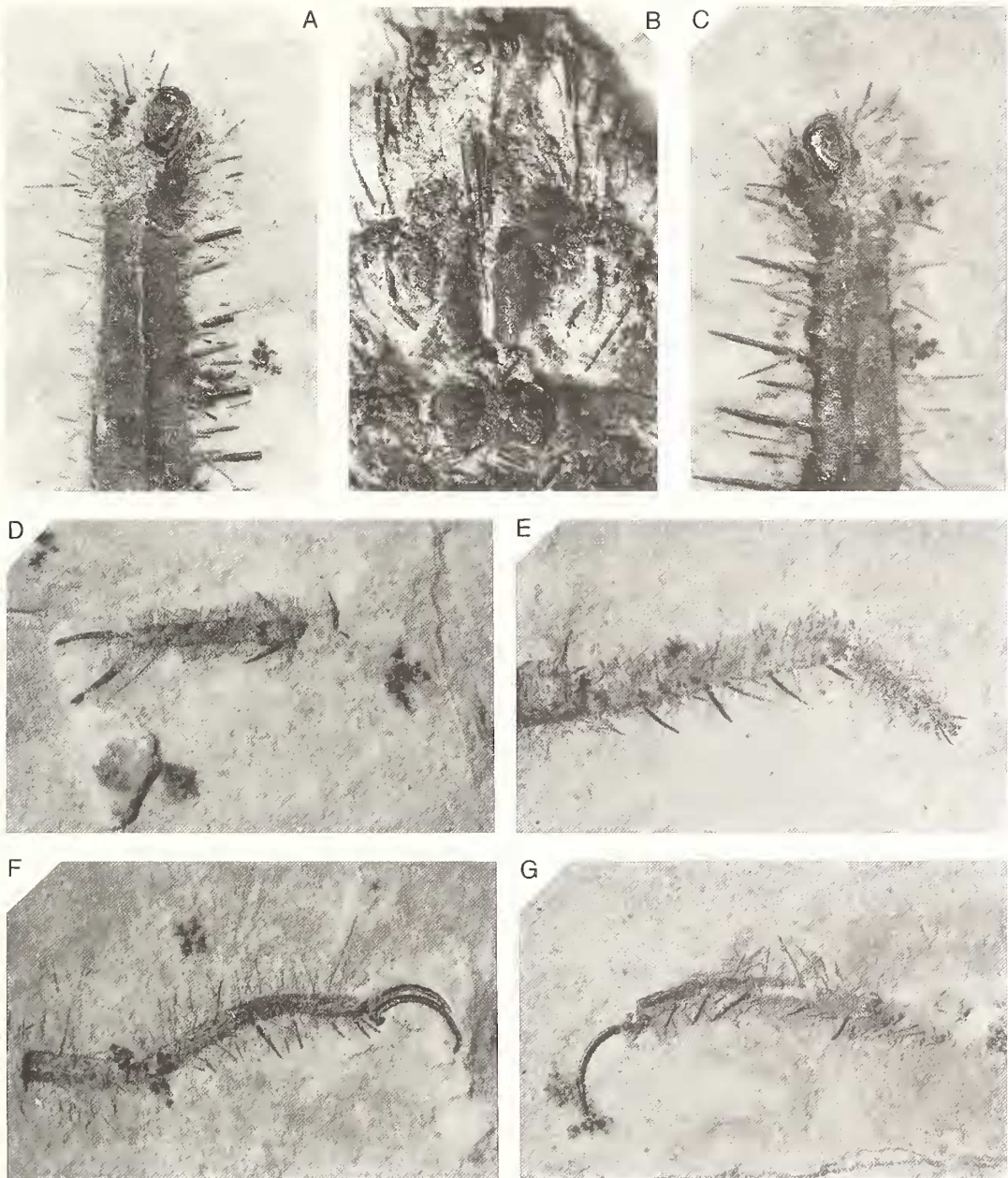
TEXT-FIG. 6. *Cratosolpuga wunderlichi* Selden, gen. et sp. nov. Holotype; Cretaceous (Aptian), Crato Formation; Ceará Province, Brazil; Sol 1. A, C, distal tibia and tarsus of pedipalp. A, left ×20; C, right ×23. B, anterior carapace margin with eyes, and basal chelicerae showing male flagella; basal section of whip of left flagellum is missing; whips disappear into matrix between cheliceral bases; ×23. D–G, tarsi of legs left III, right III, left IV and right IV, respectively; showing basitarsal spines (leg III), hairs and trichobothria, and telotarsal claws (missing from right III) with distal joint; ×15.

TEXT-FIG. 5. Camera lucida drawing of *Cratosolpuga wunderlichi* Selden, gen. et sp. nov. Holotype; Cretaceous (Aptian), Crato Formation, Ceará Province, Brazil; Sol 1 in the Wunderlich Collection. See Plate 2. Scale bar represents 10 mm.

a dorsal flagellum as seen in Gylippidae (e.g. Roewer 1934, figs 228–229, 233–234); the feature in the fossil appears more substantial than such membranous flagella, however. Thirdly, the fixed finger may have been broken or crushed and matrix (or calcite-bearing fluids, perhaps) has entered the finger. Fourthly, the dorsal side of the fixed finger is crushed down into the finger so that its dorsal side appears concave, with matrix filling the concavity. Of the second and third possibilities, the latter appears to be the more likely, since observation of modern solifuges shows that on the dorsal side of the fixed finger the cuticle is rather thinner than the lateral parts, and similar crushing of the dorsal side of the cheliceral hand can also be seen.

Dorsal and lateral parts of the movable finger can be seen in the holotype, especially on the left side, and these lie slightly outside the fixed finger and distally curve mesially towards the tip of the fixed finger. The movable finger is preserved on the second specimen, together with fragments of the fixed finger.

Flagellum. The chelicera of the holotype bears a structure known only in adult male solifuges: the flagellum. This is actually a complex of structures, which varies greatly between and within solifuge families (Roewer 1934). In some, the dorsal side of the base of the fixed finger bears a curious horn or projections. In others, there is a bunch of large setae, which may be plumose or distally expanded, and such setae may extend onto the movable finger. In many genera there is a single organ (flagellum proper, presumably a highly modified seta) which is commonly associated with groups of modified setae. This latter type is found in the fossil genus. In modern solifuges the flagellum proper may be a curved or coiled whip-like structure or may be shorter and membranous. There may be a whip-like structure with a membrane, and occasionally a variety of such structures occur on the same animal. The flagellum may be fixed or movable, in which case the movement is generally paraxial. The function of the flagellum has not been clearly established. Though confined to the male sex, it has not been observed taking part in copulatory activities.

The flagellum of *Cratosolpuga* is a straight, styliform structure on a bulbous base, with a narrow strip of membrane running the length of the spine (Text-fig. 6B). The membrane appears to have been widest at the base, where remnants of its broken edge on the base suggest it partly enveloped the base. Distal to the base, the stiff membrane is curved in a gutter-like arrangement. Gradually, towards the tip of the flagellum, the membrane dominates over the flagellar shaft, and eventually the membrane edge forms the acicular tip to the flagellum. The bulbous base is clearly set off from the chelicera, which could be evidence for its movability, but members of the family Solpugidae bear a flagellum with a bulbous base, clearly set off from the chelicera which is immovable.

The male flagellum is very distinctive and differs between species. It is a good specific character, and is always figured when new species are described in which males are known (indeed, it is not always possible to identify female solifuges). The flagellum of *Cratosolpuga* resembles somewhat that of some southern African *Blossiola* species (e.g. *B. hessei* Lawrence, 1929), in which the membrane is narrow and runs along the length of the styliform flagellum which is bent slightly only near the tip. The flagellum of these daesiids is movable. The bulbous base of the flagellum resembles that of the Solpugidae, but in this family the flagellum is fixed, and the distal, whip-like part of the flagellum always runs anteriorly for a short distance before curving backwards (the whip passes directly backwards in *Cratosolpuga*). There is no membrane running along the solifuge flagellum, which is tubular. In Ceromidae, the flagellum is movable on a bulbous base, the shaft is long, runs nearly directly backwards, and bears a thin strip of membrane running along the flagellum length. The flagellum of the ceromid *Ceroma ornatum*, studied by PAS, is very similar to that of *Cratosolpuga*, except that it curves somewhat and reaches back beyond the base of the chelicera.

Coxosternal region. The coxosternal region is seen only in the juvenile specimen (Text-fig. 3). The pedipalp coxae are large, directed anterolaterally, and come close together along straight mesial margins. The coxae of leg I are also directed anterolaterally; they do not meet mesially, but are separated by a small triangular area, presumably occupied by a sclerite in life. Sørensen (1914, pl. 1, fig. 4, ste^1) and Roewer (1934, fig. 80, St_1) figured a sternite (tritosternum according to Roewer)

in this position, and a similar structure can be seen in *Ceroma ornatum*. According to Sørensen, this conceals the suboesophagal ganglion. The more posterior coxae appear to be laterally directed, with clear gutters separating the coxae of legs II and III.

Pedipalp. The pedipalp in Solifugae consists of coxa, trochanter, femur, patella, tibia and tarsus. The limb joints seen in the fossil are almost identical to the examples shown by Roewer (1934). For example, at the pedipalp patella–tibia joint of *Cratosolpuga*, there are some approximately triangular areas of shiny, wrinkled cuticle to the mesial side of the articulation point which represent the areas labelled Gleitflächen on Roewer's (1934) figure 56, which shows the same joint in *Solpuga venator*. Examination of a specimen of *Galeodes* revealed that this cuticle is somewhat leathery, stiff but neither membranous nor rigid, and the triangular areas fold against one another rather like the zigzag folding sides of a piano accordion or an expanding document case. The true arthrodial membrane in the fossil is hidden beneath these areas of leathery cuticle.

The pedipalp tarsus of *Cratosolpuga* is short, somewhat bulbous, and broader than the tibia (Text-fig. 6A, C). The tibia–tarsus joint is distinct, especially on the mesial side of the dorsal surface. Possibly the tarsus was movable to some extent. At the inner distal tip of the tarsus is a raised area of dark, shiny, wrinkled cuticle which represents the sucker organ.

Legs. The legs of *Cratosolpuga* are rather long; the leg formula is 4132. The first leg is, as in most solifuges, long and thin, and used as a tactile organ similar to the pedipalps in other arachnids. It consists of coxa, trochanter, two femora, tibia, basitarsus and telotarsus. This leg bears no spines, only short and long fine hairs and bristles. The number of leg I tarsal claws is used in the family diagnoses of solifuges (Muma 1976); they vary from 0–2, and there is some variability within families. Early workers were unaware that these claws could be used for phylogenetic purposes, particularly as they may be tiny and hidden amongst setae and spines; for this reason they were occasionally overlooked. In *Cratosolpuga*, there is evidence for at least one small claw, in the form of a tiny, transverse spine at the distal tip of the telotarsus on the left side; on the right side, about three transverse bristles can be seen. So it is possible that these are merely bristles at the tip of the telotarsus preserved transversely, rather than true claws.

Leg II consists of coxa, trochanter, two femora, tibia, basitarsus and telotarsus. The proximal podomeres are directed upwards, so that they present their distal joints on the fossil. This is the shortest leg. The tibia bears a distal, slightly curved, spine. The basitarsus bears three slightly distally curved spines on its presumed dorsal surface, and between these are two more similar spines slightly removed from the main row towards the posterior surface. This spination is found on a number of modern solifuges. The telotarsus is poorly preserved on the left side of the holotype, but the right side shows a pair of long, curved naked claws with a joint near the tip. The telotarsus bears pairs of spines ventrally. More than one pair of spines may be present on each tarsomere, so it is impossible to count the number of tarsomeres by counting spine pairs. However, since each tarsomere generally bears at least one pair of spines, each spine pair could represent one tarsomere. Thus a maximum of four tarsomeres may be present in the telotarsus of leg II, but the lack of evidence for any joints (which are conspicuous elsewhere on the limbs) suggests that only a single tarsal segment was present.

Legs III and IV consist of coxa, trochanter, basifemur, telofemur, patella, tibia, basitarsus and telotarsus. Both legs are quite long. The telotarsus of leg III is not well preserved on the holotype, but the lack of joints suggests that only a single segment is present; if tarsomeres are present then there is a maximum of four. The telotarsus of leg IV is better preserved, and the lack of joints indicates a single segment. A pair of long, curved, naked claws with a joint near the tip is present on the tarsi of legs III and IV, as on leg II. Tarsal claws cannot be seen on the juvenile specimen; the visible tarsi are thickly clothed with setae (Text-figs 3, 6D–G).

The proximal podomeres of leg IV are poorly preserved on the holotype, but remnants of two racquet organs (malleoli) are preserved on the right side. In living solifuges, malleoli occur on the coxa (two), trochanter (two) and basifemur (one). Judging from their position, the malleoli on the

fossil represent the distal one of the trochanter and the single one of the basifemur. Only a small part of the telofemur is preserved on the left side. This podomere must be very short on the dorsal side of the holotype, given the length of the dorsal side of femur 2 (seen on the left side) and the position of the posteriormost malleolus which would have been situated on the basifemur. On the juvenile specimen, long trichobothria can be seen extending from tibiae IV (Text-fig. 3).

Opisthosoma. The abdomen is well preserved only on the juvenile specimen (Text-fig. 3). Ten segments can be counted from between the coxae of the fourth leg to the rear of the animal. The second of these appears to consist of a pair of lobes, and probably represents the operculum. The following segments are revealed by paired dark lateral corners and rows of setae. The more anterior post-opercular segments appear to be rectangular, the more posterior become increasingly backwardly curved, so that the most posterior is suboval in shape. This segment bears some long setae.

DISCUSSION

The most comprehensive survey of the Solifugae was that of Roewer (1934), which, although an indispensable reference to this arachnid group, is so plagued with inaccuracies and takes such a strict typological approach to systematics that most later workers have experienced severe difficulties in applying Roewer's scheme. Muma (1976) reviewed solifuge families in an attempt to reconcile the situation. His scheme, whilst only tentative, and following Roewer in many aspects, is the most recent 'best guess' at a familial taxonomy, and is followed herein. Some additional information on American families was provided by Maury (1984), and a recent update of Muma's scheme incorporating Maury's changes is given in El-Hannawy (1990).

Some solifuge families are defined by distinct autapomorphies, such as the digging adaptations of the Hexisopodidae, and the hairy claws of Galeodidae, which *Cratosolpuga* lacks. The most useful morphological feature in solifuge taxonomy is the form of the male flagellum. A number of main types can be recognized which can be used to distinguish families. Mesiodorsally placed styliform flagella are found in Solpugidae, Ceromidae, and Daesiidae. Hewitt (1919) discussed the evolutionary development of the flagellum in a survey of the South African solifuges. He regarded the flagellum of daesiids (*Daesia, Blossia, Melanoblossia, Hemiblossia, Gluviopsis*), which consists of a membrane with infolded edges which unite at the base to form a cup, to be relatively primitive, and the ceromid flagellum to be derived with respect to that of daesiids. It is movable, styliform and bears a narrow membrane which forms a gutter along the length of the flagellum. The most advanced flagellum in this scheme belongs to Solpugidae, which has a fixed, bulbous base and a long tube (formed by fusion of the edges of the gutter, according to Hewitt) which basally runs forwards along the fixed finger before curving backwards. The American solifuge *Syndaesia* Maury, 1980 bears a tubular flagellum, yet it was placed in Daesiidae by Maury (1980) on account of the movability of the flagellum, the lack of tarsomeres, and other features. The flagellum of *Cratosolpuga*, with its basal bulb, backwardly directed whip and narrow membrane running along its length, is clearly closest in morphology to that of Ceromidae.

The propeltidium of *Cratosolpuga* is wider than long, with distinct lateral lobes that appear to be free anteriorly but fused posteriorly. There is no distinct median divide, as seen in some solifuges. The arci posteriori are raised high above the rear of the propeltidium in the fossil, and the first abdominal tergite is semicircular, with radiating spines around its edge. The eyes are raised on a common tubercle, which bears a pair of prominent, forwardly directed spines. The propeltidium of *Blossia sabulosa* is longer than wide and has a prominent median divide; the first abdominal tergite is bilobed, with radiating setae. The propeltidium of *Ceroma ornatum* is wider than long, the median divide appears only as faint pigmentation; tergite 1 is broadly semicircular. The exterior lobe is anteriorly free and posteriorly attached in both ceromids and daesiids. Overall, the propeltidium and related structures of *Cratosolpuga* more resemble those of ceromids than daesiids.

The presence or absence and, if present, the number of tarsal claws on leg I helps to define families. These vary from none to two. *Cratosolpuga* possibly bears a small leg I tarsal claw.

Solpugidae bear none, Ceromidae two, and Desiidae none or one. The number of segments in the tarsi of legs II to IV is a useful character. The tarsal segment formula (II, III, IV) of *Cratosolpuga* is probably 1, 1, 1, but could be more if the joints are hidden. The formula for Solpugidae is 4, 4, 6/7, for Ceromidae 1, 2, 2, and for Daesiidae 1–2, 1–2, 1–4. The additional tarsal segment in the ceromid *Ceroma ornatum* is short, whilst those of daesiids are rather longer (e.g. Roewer 1934, fig. 274). The paired claws of legs II to IV are situated on a small apotele which in some families, such as Ceromidae and Solifugidae, bears a distinctive pulvillus (= arolium, empodium, onychium, plantium; see Roewer 1934, figs 69–70; Muma 1951, figs 264–270). The tarsal pulvillus of the male of *Ceroma ornatum* studied is large and bifid (see also Roewer 1934, fig. 70), but the female *Ceroma ornatum* studied lacks the pulvillus. The presence of a pulvillus, therefore, is not diagnostic for Ceromidae. Daesiids bear no pulvillus, but in *Blossia sabulosa* there are rows of bristles associated with the claws. The tarsal claws of *Blossia sabulosa* are long, and those of leg IV exceed the length of the telotarsus; in *Ceroma ornatum* the tarsal claws are rather shorter but increase in length from leg I to leg IV. The tarsal claws of *Cratosolpuga* are closer in length to those of the ceromids.

An anteriorly free but posteriorly fused exterior lobe of the propeltidium, as found in *Cratosolpuga*, is characteristic of the families Karschiidae, Solifugidae, Eremobatidae, Ceromidae, Galeodidae and Amacataidae (included in Daesiidae by Maury 1980) (Muma 1976). Other features of the prosomal tergites appear not to be important in solifuge phylogeny.

The cheliceral hands of Ceromidae are distinctly high, dropping at the base of the fixed finger; this feature is found also in *Cratosolpuga*. The pedipalp of *Cratosolpuga* bears prominent spines along its inner edges, presumably to aid in prey capture. The *Ceroma* specimen studied has spines in a similar arrangement but they are rather finer. Similarly, the dense arrangement of thick spines on the propeltidium and chelicerae of *Cratosolpuga* are matched in the modern solifuges studied, but appear rather finer. Possibly the replacement by dense, dark goethite makes them appear more prominent in the fossil than the hyaline spines seen in modern specimens under alcohol.

Leg spination can be of phylogenetic value in solifuges. *Cratosolpuga* bears many spines on the pedipalps. Spinose pedipalps are characteristic of Galeodidae (e.g. Roewer 1934, fig. 315). Ceromids bear long, fine spines in a similar arrangement to *Cratosolpuga* on their pedipalps; some daesiids bear short spines on the pedipalps (e.g. Roewer 1934, fig. 254), whereas others bear long spines (e.g. Roewer 1934, fig. 259); *Blossia sabulosa* has only fine setae.

In conclusion, *Cratosolpuga* is placed in Ceromidae, based on the cheliceral flagellum, the shape of the propeltidium, the eye tubercle, leg spination, and other features. It differs from a typical *Ceroma* male in lacking tarsal pulvilli, and in having only a single tarsal segment on all legs. We consider this placement to be the most appropriate in view of the current state of solifuge systematics, and particularly the lack of a modern, cladistic assessment of familial relationships.

The present-day distribution of solifuges reflects that of deserts, with the exception of Australia and China, where solifuges have yet to be found. This correlation explains the lack of solifuges in most of Brazil and West Africa today, where the dominant habitat is tropical forest. The Chapada do Araripe is situated at about 8° S, and was situated at about the same latitude during mid-Cretaceous times (Smith *et al.* 1981). However, north-east Brazil was located in the centre of a continent in the mid-Cretaceous, and may have experienced a more arid climate than today. Whilst the great diversity and abundance of plant and animal fossils in the Crato Formation attest to a rich biota adjacent to the lake, there is some evidence for a drier climate in the surrounding area. Grimaldi and Maisey (1990) noted the presence of xerophilic arthropods such as Asilidae (Diptera), Myrmeleontidae (Neuroptera) and scorpions as evidence for a drier hinterland to the lake, da Silva (1986) deduced that the lake was saline and landlocked, at least during the later parts of its history, on the evidence of evaporites in the sequence, and Maisey (1990) noted that Gnetales pollen and macrofossils suggested an open, arid environment. The presence of a solifuge adds weight to the hypothesis of an arid palaeoenvironment during deposition of the Crato Formation; though the presence of *Protosolpuga* in Mazon Creek, which represents a tropical forest community, indicates that solifuges have not been confined to arid environments throughout the whole of their geological history.

If Hewitt (1919) is correct in his assumption that the trend in evolution of the male flagellum is from an open cup (Daesiidae) to an elongate, gutter-like form (Ceromidae) to an enclosed tube (Solifugidae), then the phylogenetic relationship (Daesiidae(Ceromidae + Solpugidae)) is implied. Ceromidae are confined to southern Africa at the present day; Daesiidae are known from Africa, southern Europe, the Middle East, and South America. The presence of a ceromid in the Cretaceous means that the split between the sister lineages Daesiidae and (Ceromidae + Solpugidae) had occurred before this time. The disjunct distribution of daesiids at the present day suggests an earlier widespread occurrence of that family. The origin of the ceromid + solifuge clade may have occurred during the initial rifting events of Pangaea to form the proto-Atlantic ocean in the Cretaceous, since fragmented land masses in the rifting zone would have led to speciation events. Later, changes in the climate adjacent to the new ocean could have caused extinction of solifuges from the areas now occupied by Brazil and West Africa. The predominantly African distribution of Solpugidae at the present day (none is known from South America), concurs with the hypothesis of the development of this family from Ceromidae, or a common ancestor, after the rifting event.

SYSTEMATIC PALAEONTOLOGY

Order SOLIFUGAE Sundevall, 1823

Genus PROTOSOLPUGA Petrunkevitch, 1913

Remarks. The diagnosis presented by Petrunkevitch (1913) is partly incorrect and quite inadequate for separating this animal from any other solifuge genus. The only 'feature' distinguishing this fossil from any other solifuge is the fact that it is Carboniferous; all other known solifuges are Cretaceous or younger. A new family, Protosolpugidae, was erected for this specimen by Petrunkevitch (1953) without discussion. Two years later, he placed it provisionally in Galeodidae Pocock, 1897, an assignment which was 'entirely arbitrary and was motivated by the fact that this family has a wide Old-World distribution' (Petrunkevitch 1955, p. P154). Since it cannot be supported by any real evidence, we prefer not to assign the fossil to any modern solifuge family.

Protosolpuga carbonaria Petrunkevitch, 1913

Plate 1, figures 1–2; Text-figure 2

1913 *Protosolpuga carbonaria* Petrunkevitch, p. 74, fig. 40.
1949 *Protosolpuga carbonaria* Petrunkevitch, p. 292.
1953 *Protosolpuga carbonaria* Petrunkevitch, p. 112.
1955 *Protosolpuga carbonaria* Petrunkevitch, p. P155, fig. 112,3.

Material. Holotype and only known specimen, 00155/B1336 in the Peabody Museum, Yale University, New Haven, Connecticut. The specimen is from the Late Carboniferous (Westphalian D) Francis Creek Shale of Mazon Creek, Illinois.

Remarks. See remarks above for the genus, of which this is the type and only known specimen.

Description. See *Morphological interpretation*, above.

Family CEROMIDAE Roewer, 1934

Remarks. The cheliceral flagellum of the Cretaceous is clearly ceromid in character, as are many other features, such as the shape of the propeltidium, the eye tubercle, leg spination, etc. The fossil genus differs from a typical *Ceroma* male in lacking tarsal pulvilli (though this is not a diagnostic character), and in having only a single tarsal segment on all legs.

Genus CRATOSOLPUGA Selden gen. nov.

Derivation of name. From the Crato Formation, the stratum in which the fossil was discovered, and *Solpuga*, a typical genus of Solifugae.

Type species. Cratosolpuga wunderlichi Selden, sp. nov., by monotypy.

Diagnosis. Male cheliceral flagellum attached to dorsomedial side of chelicera near base of fixed finger, consisting of globose base and styliform whip extending directly backwards to base of chelicera, stiff membrane partly enclosing flagellum base and running length of flagellum forming a narrow gutter. Single tarsomere on all legs.

Cratosolpuga wunderlichi gen. et sp. nov.

Plate 1, figures 3–4; Text-figures 4–6.

Derivation of name. In honour of Jörg Wunderlich, who recognized the importance of the holotype specimen and sent it to PAS for study.

Material. Holotype specimen, part only, No. Sol 1 is deposited in the collection of J. Wunderlich, Straubenhardt, Germany. Additional (presumed juvenile) specimen (not to be regarded as a paratype), part only, No. SMNK 1268 PAL in the Staatliche Museum für Naturkunde, Karlsruhe, Germany. Both are from the Crato Formation, Lower Cretaceous (Aptian) of the Chapada do Araripe, Ceará Province, north-eastern Brazil.

Diagnosis. As for the genus.

Description of holotype. Medium-sized solifuge (Text-fig. 5). Propeltidium anterior margin nearly straight mesially, curving gently backwards towards lateral, exterior lobes separated from propeltidium anteriorly, fused to propeltidium posteriorly. Anterior margin a definite ridge which extends to point where exterior lobe is fused. Posterior margin of propeltidium approximately semicircular. Total width of propeltidium (including exterior lobes) 3·3 mm, length 1·9 mm. Eyes at anterior edge of propeltidium, each on a radially ridged, raised lobe, these lobes both situated on a common eye tubercle; lens diameters about 0·23 mm and about a diameter apart, rugose cuticle between and around eye tubercles. One pair of short spines emerges from between the eyes and points anterolaterally; another pair occurs beneath these. Propeltidium thickly clothed with spines. Exterior lobe raised into pyramidal shape (broken on right side). Median plagula of propeltidium not distinct from anterior arci. Posterior arci of parapeltidium transverse. Junction between anterior and posterior arci of parapeltidium forms prominent transverse ridges. Parapeltidium thickly clothed with spines. Mesopeltidium a distinct semicircular tergite, deeply concave with raised anteromesial area and raised rim; a row of large spines radiate from the tergite around its rim. Metapeltidium and dorsal opisthosoma not preserved. Only a few, scattered hairs mark the impression of the ventral opisthosoma between the femora of legs IV.

Chelicerae 3·3 mm long, basal body 2·3 mm long, globose, pyriform, as high as, or higher than, propeltidium (but somewhat crushed in fossil). Thickly clothed with thick spines; two very large spines present on posterolateral dorsal surface, directed backwards over anterior border of propeltidium. Long, forwardly directed spines on anterior part of body. Long, fine setae present near base of flagellum. Fixed finger incomplete. Movable finger appears slightly lateral to fixed finger, with mesially curved tip. Flagellum situated on dorsal surface of chelicera at base of fixed finger. Flagellum a backwardly directed, styliform structure, with globose base. Narrow membrane at first partially enclosing base, then running the length of flagellum on the exterior side. Membrane forms a gutter-like structure, the membrane edge distally dominating the formation of the acicular flagellar tip.

Pedipalps robust, forwardly directed, with many long spines on mesial surfaces of trochanter, femur, patella and tibia. Podomeres thickly clothed with fine spines, long trichobothria also present. Trochanter appears as triangular feature adjacent to chelicera; two spines project forward. Femur with row of about six large spines on mesial surface, with smaller spines between, the larger ones increase in length (longest exceeding thickness of podomere) from the base to about two-thirds of podomere length, then decrease. Distal joint bears large triangular area of leathery cuticle on mesial side. At least four prominent spine bases occur in distal half of

dorsal surface. Right femur has some cuticle broken away from the dorsal surface, revealing a tendon. Patella bears about six large spines on the mesial surface, which increase in length towards middle of podomere (longest exceeding thickness of podomere), with shorter spines between. Two prominent spine bases occur at mid-length on the dorsal surface. Large area of leathery cuticle stretches across mesial side of pa–ti joint. Tibia bears a row of five (possibly six) large spines alternating with shorter spines, themselves with smaller spines between, and there is a thick clothing of long, fine hairs. At least two large spine bases are present on the dorsal surface at about mid-length. Distal tibia joint is distinct; little constriction in width of the tibia at the joint. Marked edge to end of tibia at inner side of ti–ta joint, outer side shows wrinkled cuticle. Tarsus short, somewhat bulbous, broader than tibia distally, and probably movable. Tarsus bears many thin spines, and a large sucker at the tip. Podomere lengths (in mm): tr 0·8; fe 5·2; pa 5·1; ti 3·5; ta 1·0.

Leg I thickly clothed in short and long, fine bristles but no thick spines. Short trochanter bears at least two spines dorsally, and short first femur distinctly narrower dorsally than elsewhere. Second femur long, tibia slightly longer than second femur, basitarsus shorter than these podomeres. Telotarsus about half the length of basitarsus and bearing stout bristle(s) at tip which may include claw(s). Podomere lengths (in mm): tr ⩾ 0·5; fe 1·2 (max.); pa 4·1, ti 4·2; ta1 2·9; ta2 1·5.

Leg II stouter than leg I but is shortest of all legs. Clothed in many fine hairs or bristles (as evidenced by the density of follicles seen on the dorsal surface) and bearing some stout (but where preserved rather short) spines. Trochanter presented with its distal joint uppermost in the fossil, and the short first femur is similarly disposed, so it is impossible to provide meaningful lengths for podomeres. Trochanter bears at least two spines dorsally. Patella relatively short, and tibia about the same length. Patella bears two prominent spine bases at one-third and two-thirds the length of the podomere on its dorsal side, distalmost is the larger. Smaller spine bases scattered across the dorsal surface. Prominent articulations at the proximal pa joint (dorsal) and distal pa joint (anterodorsal); latter joint shows an area of leathery cuticle across the joint on the anterior side. Slightly curved spine on the anterior side of the distal joint. Basitarsus slightly shorter than the preceding two podomeres and shows articulation dorsally at distal joint. A row of five stout, gently distally curved, spines occurs on dorsal surface, second and fourth spines slightly removed towards the posterior surface. Spine opposite fourth dorsal spine on anterior surface. Telotarsus approximately half length of basitarsus. On both sides, telotarsus is bent posteriorly; it bears bristles and paired spines ventrally. Telotarsus probably a single segment, but if composed of tarsomeres than a maximum of four is present. Pairs of long, curved, naked claws present; each bearing a joint near the tip. Podomere lengths (in mm): pa 2·8; ti 2·5; ta1 1·9; ta2 1·1 (excluding claws; claws c. 0·8).

Leg III longer than leg II, and as stout, but shorter than leg I. Thickly clothed with long bristles and short and long spines. Trochanter appears slightly larger than that of leg III, but is not well enough preserved to estimate quantitative size. Basifemur short, and narrower dorsally than ventrally. Dorsal side bears large spines (one is present on the left side, at least one more is apparent from preserved spine bases). Femora are bisected on both sides by a crack in the specimen. Distal joint of patella bears an articulation anterodorsally and an area of leathery cuticle anterior to this. Tibia shorter than patella and less stout. It bears some long spines anteriorly and one large spine base medially on the dorsal surface. Basitarsus shorter than tibia; it is thickly clothed with bristles and bears rows of spines. Telotarsus shorter than basitarsus, and similarly clothed with bristles and pairs of spines. Telotarsus appears to be a single segment, but if tarsomeres present then a maximum of four. Two long, curved, naked claws are present, each bearing a joint near the tip. Podomere lengths (in mm): fe1 0·7; fe2 + pa c. 4·9; ti 3·8; ta1 2·5; ta2 1·4 (excluding claws; claws 0·8).

Leg IV the longest. Thickly clothed with hairs, long bristles, and spines. Proximal podomeres poorly preserved, but remnants of two racquet organs (malleoli) preserved on the right side. Judging from their position, these belong to the trochanter and basifemur (distal). Only a small part of the telofemur is preserved on the left side, very short dorsally. Patella large; only some ventral bristles are preserved on the right side but left one fully preserved. It bears long, thin, slightly curved spines, in addition to fine bristles, apparently on all surfaces. Distal joint shows an articulation on the side which is now dorsal; leathery cuticle present anterior to this. Tibia is about as long as patella but thinner; bears short spines and bristles. Basitarsus shorter than tibia but similarly clothed in fine spines, hairs, and bristles. Telotarsus bears fine bristles, long hairs, and paired spines, and appears as a single, curved segment; if tarsomeres present then maximally seven. Pair of naked, curved claws present on a small apotele; each claw has a joint near the tip. Podomere lengths (in mm): pa 5·3; ti 5·0; ta1 3·7; ta2 2·2 (excluding claws; claws 1·0).

Description of additional specimen. Small (5·8 mm long including chelicerae) specimen, presumed to be juvenile, and almost all parts of body preserved (Text-fig. 3). Specimen shows predominantly ventral structures seen from the dorsal (internal) aspect. Free fingers of chelicerae expand slightly anteriorly to mid-length, then taper

to a slightly curved point. A fragment of fixed finger overlies each movable finger. Pedipalp coxae large, trapezoidal, straight mesial edges run parallel in midline, parallel anterior and posterior edges subtend an angle of 40° from the midline. Leg I coxa parallel to pedipalp coxa, but without straight mesial edge. Coxae I do not meet mesially, but are separated by a small triangular sclerite with apex anterior. Coxae II and III transverse. Coxae IV poorly preserved. Pedipalp patella with two, parallel rows of about four long spines, tibia with more, irregularly arranged long spines. Richly clothed in long, fine setae and some trichobothria. Short telotarsus. Approximate podomere lengths (in mm): fe 1·4; ti 1·4; ta1 1·4; ta2 0·5. Leg I thin, mostly obscured by pedipalp. Richly clothed in long, fine setae and some trichobothria. Leg II short, at least seven short spines on basitarsus and telotarsus, telotarsus thickly clothed with setae, claws not seen. Approximate podomere lengths (in mm): fe 0·4; pa 0·6; ti 0·6; ta1 0·7; ta2 0·5. Leg III longer than leg II, two large spines on distal end of tibia, tarsal claws not seen. Approximate podomere lengths (in mm): fe2 0·4; pa 1·0; ti 0·9; ta1 0·9; ta2 0·6. Leg IV collapsed proximally, proximal podomeres poorly preserved, malleoli not seen. Proximal and distal pairs of long spines on basitarsus, at least one pair of long spines on telotarsus, claws not seen. Telotarsus thickly clothed with setae, long trichobothrium on tibia. Approximate podomere lengths (in mm): ti 0·8; ta1 0·6; ta2 1·0. Ten abdominal segments. Second bilobed, third to sixth subrectangular, more posterior become increasingly backwardly curved, so that tenth is suboval. Tenth (anal) segment bears long setae.

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